

Restoring riparian meadows currently dominated by *Artemisia* using alternative state concepts – above-ground vegetation response

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Abstract. Livestock overgrazing and stream incision in the western USA often result in encroachment and dominance of *Artemisia tridentata* ssp. *tridentata* (Big sagebrush) in riparian areas that formerly supported meadows. To define the alternative states and thresholds for these ecosystems, we conducted a restoration experiment that included sites with high, intermediate or low water tables. We used a paired-plot approach in which one plot on each site was burned and seeded with native grasses and forbs typical of naturally occurring dry meadow and *Artemisia/Leymus cinereus* ecological types, while adjacent unburned plots served as controls. Sites with high and intermediate water tables had greater initial abundances of perennial grasses typical of dry meadows, such as *Leymus triticoides* and *Poa secunda* ssp. *juncifolia*, and these species increased after the burn. In contrast, sites with low water tables were dominated by annual forbs such as *Chenopodium album* and *Descurainia pinnata* after the burn. Biomass increased progressively from 1997 to 1999 on burned plots, while controls showed little change. Burning effects were microsite specific, with former *Artemisia* microsites exhibiting lower biomass than interspaces initially, but similar or higher biomass by the third year. Establishment of seeded species was low and species composition was determined largely by pre-burn vegetation. *Artemisia* dominated sites with high water tables appear to represent an alternative state of the dry meadow ecological type, while sites with low water table sites have crossed an abiotic threshold governed by water tables and represent a new ecological type. Burning is an effective tool for restoring relatively high water table sites, but low water table sites will require burning and seeding with species adapted to more xeric conditions.

Keywords: Above-ground; Biomass; Dry meadow; Great Basin; Species composition.

Nomenclature: Hickman (1993); Cronquist et al. (1994).

Introduction

In the semi-arid Great Basin of the western USA, riparian ecosystems represent a valuable but often degraded resource. Many upland stream systems are in an incisional phase due to past climate changes (Miller et al. 2001). Anthropogenic disturbances, including overgrazing by livestock and road construction within riparian corridors, have adversely affected the ecological condition of these ecosystems (Belsky et al. 1999) and increased the rate and magnitude of stream incision (Chambers et al. 1998). These disturbances, in combination with lowered water tables, have facilitated encroachment and dominance of the shrub *Artemisia tridentata* ssp. *tridentata* (Big sagebrush) in grass- and sedge-dominated meadows and resulted in homogenizing the landscape (Chambers & Linnerooth 2001). Restoring a mosaic of meadow and sagebrush dominated ecosystems would improve watershed functioning, increase biodiversity and enhance other resources.

Linear successional models are often inadequate for assessing the restoration potential of degraded ecosystems because these models imply that the ecosystems are capable of recovering to the original condition. In many cases, there is no change in condition after the stressor is removed, or the change that does occur is not a reversion to the former condition. Alternative state and transition models have been used to explain multiple or divergent successional pathways in range science (Westoby et al. 1989; Laycock 1991; Friedel 1991; George et al. 1992; Tausch et al. 1993; Rodriguez Iglesias & Kothman 1997; Rietkerk & van de Koppel 1997; Allen-Diaz & Bartolome 1998) and restoration ecology (Hobbs & Norton 1996; Whisenant 1999). Restoration experiments can be used to identify the alternative states and thresholds that exist for degraded ecosystems based upon abiotic and biotic responses to the treatments, and to determine appropriate restoration strategies for the different states (Chambers 2000a; Chambers & Linnerooth 2001).

In riparian areas, a primary determinant of the potential of a site to support a given vegetation community or alternative state is the hydrologic regime as indicated by depth to the water table. The hydrologic regime influences plant species physiological responses and competitive interactions (Martin & Chambers 2001, 2002) and community composition (Castelli et al. 2000) in Great Basin riparian ecosystems. A classification of ecological types (similar to vegetation types) exists for our study area in the central Great Basin and is based on topographic position, soil characteristics and plant species composition (Weixelman et al. 1996). Two naturally occurring ecological types appear to represent the restoration potential for riparian corridors that are currently dominated by *Artemisia*; the dry meadow type which is characterized by relatively high water tables and is dominated by grasses, sedges and forbs and the *Artemisia/Leymus cinereus* type that has relatively low water tables and is dominated by *Artemisia* and *L. cinereus* with lesser amounts of grasses, sedges and forbs (Weixelman et al. 1996). If an abiotic threshold controlled by water table has not been crossed the *Artemisia* dominated sites might represent an alternative state of the dry meadow ecological type. If a threshold has been crossed, they might be an alternative state of the *Artemisia/Leymus* type.

Fire is a major factor initiating transition in *Artemisia*-dominated ecosystems (Laycock 1991) and, because the shrub is not fire tolerant, burning may be an effective tool for restoring riparian corridors currently dominated by *Artemisia*. The initial plant species composition and environmental characteristics, including depth to water table, affect seedling establishment (Chambers & Linnerooth 2001) and regrowth of native grasses, sedges and forbs following burning. Fire influences both plant establishment processes and species interactions through its effects on soil properties, including infiltration, temperatures and nutrients (Whelan 1995). In addition, *Artemisia* plants affect micro-environmental conditions and soil chemical and physical characteristics, these differences persist even though burning eliminates the plants (Blank et al. 1994, 1998). Relative to adjacent interspaces, micro-environments under *Artemisia* canopies are characterized by lower irradiance and soil temperature and higher humidity (Burkhardt & Tisdale 1976). Soils have higher infiltration and soil water holding capacities, higher organic matter and total nitrogen contents and higher concentrations of nutrients (Doescher et al. 1984; Evans & Ehleringer 1994; Chambers 2001b). The differences between interspaces and under shrub canopies may be large enough to cause differential regrowth or seedling establishment between the two microsites (Lamont et al. 1993) and among species (Chambers & Linnerooth 2001).

In this study, we conducted a restoration experiment to identify the alternative states and define the thresholds for riparian corridors currently dominated by *Artemisia*. We hypothesized that the threshold for restoration to grass and sedge meadows could be defined largely by water table depth. A burning and seeding treatment was applied to sites with low, intermediate and high water tables to remove *Artemisia* and to assess the potential for re-establishing native grass, sedge and forb species. We addressed three specific questions: 1. Do basal cover, plant biomass and community composition differ among sites with low, intermediate and high water tables? 2. What are the basal cover, plant biomass and community responses to burning and seeding? 3. Do *Artemisia* plants (under shrub and interspace microsites) influence the observed responses?

Methods

Study site selection and experimental design

Five study sites were located in the Toiyabe Mountain Range of central Nevada that represented a gradient of modification of the dry meadow ecological site type. Site selection was based on presence of herbaceous understorey species representative of the dry meadow and *Artemisia/Leymus* ecological types (Weixelman et al. 1996) and depths to water table were determined from hand-augered wells. All sites occurred on drainage ways and stream terraces at elevations ranging from 2000 to 2300 m a.s.l. and were characterized by haplocryoll soils. The following sites were included:

Wet sites; water table – 60 to – 250 cm;
Willow Creek at 39° 33' 12" N, 116° 59' 30" W;
Ledbetter Creek at 39° 45' 30" N, 116° 59' 30" W;
Intermediate site; water table – 100 to – 280 cm;
Willow Creek (39° 33' 28" N; 117° 30' 00" W);
Dry sites; water table – 280 to – 300 cm;
Willow Creek at 39° 33' 12" N, 116° 59' 30" W;
Marysville Creek at 39° 02' 30" N, 117° 24' 27" W.

Wet and intermediate sites had higher cover of perennial graminoids and forbs, lower densities and volumes of *Artemisia* and were more similar to the dry meadow ecological type than low water table sites (Linnerooth et al. 1998). Perennial understorey species on the study sites included *Carex douglasii*, *Leymus cinereus*, *L. triticoides*, *Poa secunda* ssp. *juncifolia* and *Lupinus argenteus*. Common annual species included the native forbs *Collinsia parviflora*, *Mimulus suskendorfii*, *Phlox gracilis* and the exotic grass *Bromus tectorum*.

At each site a paired plot approach was used in which one plot received the restoration treatment (burning and seeding) while the other plot served as the control. Burning took place from October 19–21, 1996

by Humboldt-Toiyabe National Forest personnel. Drip-torches were used to ignite fires that removed all shrubs and herbaceous vegetation. Study sites varied from 740 m² to 900 m² and were fenced to prevent livestock grazing.

Burned plots received a one-time broadcast seeding of native perennial grasses and forbs that included species typical of the dry meadow and *Artemisia/L. cinereus* ecological site types. The species were *P. secunda* ssp. *juncifolia*, *L. cinereus*, *L. triticoides*, *Agropyron smithii*, *Muhlenbergia richardsonis*, *Achillea millefolium* and *Linum lewisii*. Commercial seed lots were used for all species except *P. secunda* ssp. *juncifolia* which was collected from nearby meadows. Both collected and purchased seed were tested for viability using standard tetrazolium tests prior to calculating seeding rates. Each species was broadcast at a rate of 100 viable seeds.m⁻² (total = 600 seeds.m⁻²) and then raked into the soil.

Environmental data and vegetation response

Three to four piezometers (2.54 cm diameter metal conduit with the lower 50 cm slotted) were installed in burned and control plots in August 1997 at depths > – 300 cm to measure water table depths during the growing season. Rain gauges were installed at each site (except for Willow dry, due to its proximity to Willow wet) to measure cumulative precipitation.

A stratified random design was used to sample the above-ground vegetation response. For understorey vegetation 20 quadrats (0.25 m²) were located randomly in former or present under shrub canopies (under shrub microsites) and between shrub canopies (interspace microsites) in burned and control plots (20 quadrats × 2 microsites = 40 quadrats per water table/treatment combination). Sampling was conducted at peak production in early July 1997, 1998 and 1999. All sample locations were marked to avoid resampling the same areas. Biomass and species composition data were obtained by clipping each species within a sampling quadrat to ground level and oven drying (60 °C). Percentage basal cover (vegetation, bare ground, gravel, rock, litter) was determined using a point frame (0.5 m long, 10 points).

Shrub volumes calculated from the pre-burn and 1999 data were used to analyze shrub response to the burning and seeding treatment. Prior to conducting the burning and seeding treatments the height, maximum and perpendicular diameter and basal diameter of the shrub species were measured to determine shrub volumes (Linnerooth et al. 1998). A stratified random design was used and all shrubs within 1-m² quadrats were measured (20 quadrats for both burned and control plots). Shrub abundance was low on burned plots in 1997 and 1998 and shrubs were included as part of the herbaceous vegetation sampling for these sample peri-

ods. In 1999 shrub regrowth via root-sprouting and seedling establishment was measured in under shrub and interspace microsites of the burned plots using the same methods as before the burning and seeding treatment. Volumes were calculated using the following equation: ($\pi/6$) * maximum diameter of shrub * perpendicular diameter of shrub * height of shrub.

Statistical analysis

The study design was a split-split plot in which the main plot factor was completely randomized. Water table depth was the main-plot factor, burning treatment the split-plot factor and microsite the split-split plot factor. Year was treated as a repeated measure. The main-plot error term was site within water table.

Data for the 3-yr study were analysed to determine differences in above-ground herbaceous vegetation recovery and shrub reestablishment. Differences in total mean biomass, biomass by lifeform and basal cover were examined using four-way (water table, treatment, microsite and year) ANOVA. Differences in pre-burn and 1999 shrub volumes among water tables and microsites on the burned plots were examined using two-way (water table and microsite) ANOVA. Mean comparisons were performed using least squares means. Species correlations (similarity) between microsites within treatment/water table combinations were examined using year-three biomass values for the 15 most abundant species sampled and Spearman's rank coefficients (R_s).

Table 1. Precipitation data for each study site for 1997, 1998 and 1999. Values are totals (cm). Overwinter is from October through May. Growing season includes June through September.

Site Period	1997	1998	1999
Willow Wet and Dry			
Overwinter	28.5	35.0	32.0
Growing season	12.3	26.0	3.0
Total	40.8	61.0	35.0
Willow Intermediate			
Overwinter	35.0	43.8	32.5
Growing season	10.8	28.0	6.5
Total	45.8	71.8	39.0
Ledbetter Wet			
Overwinter	22.0	41.5	26.5
Growing season	13.0	17.0	6.5
Total	35.0	58.5	33.0
Marysville Dry			
Overwinter	19.0	28.3	24.0
Growing season	12.2	14.0	14.0
Total	31.2	42.3	38.0

Results

Environmental data

Precipitation measured during the study varied among sites from 31–46 cm in 1997, a dry year, to 42–72 cm in 1998, a relatively wet year (Table 1). All sites received most of their annual precipitation (70%) during the winter months. The intermediate site received the highest mean precipitation (52 cm), followed by the Willow wet and dry sites (46 cm), Ledbetter Wet site (42 cm) and Marysville dry site (37 cm).

In general, water table depths were highest in spring/early summer and decreased during the growing season (Fig. 1). The Willow wet site consistently had the highest water table depths. The Ledbetter wet site had the greatest variability in water tables (–35 cm to –59 cm) over the 3 yr study. The Intermediate site had water table characteristics similar to, but deeper than, the Willow wet site. Water table depths on the dry sites generally exceeded the 300 cm depth of installed wells. Burn and control plots on the different sites had consistently higher or lower water tables, except on the Willow wet site (Fig. 1).

Basal cover, total biomass and shrub volume

Following the burn, basal cover of vegetation and gravel/rock did not differ among years, water tables or microsites. Litter increased from year one to year two and again from year two to year three for all sites (year*treatment, $F_{2,16} = 16.03$, $P = 0.0002$) (Fig. 2). The intermediate site had higher litter cover than the wet or dry sites in all years (treatment*water table, $F_{2,2} = 40.47$, $P = 0.0241$). Conversely, percent bare ground was consistently higher on the wet and dry sites than on the intermediate site (water table, $F_{2,2} = 21.92$, $P = 0.0436$). Burned plots had greater percentages of bare ground than control plots in 1997 and 1998, but had bare ground levels similar to the controls in 1999 (year*treatment, $F_{2,16} = 22.05$, $P = 0.0001$). There were no differences between microsites for any of the different cover categories.

Wet and dry sites exhibited a three-fold increase in biomass between the first and second year after burning. Biomass doubled again between the second and third year for these sites (year*water table, $F_{2,16} = 5.29$, $P = 0.0066$) (Fig. 3). Biomass on the intermediate site was higher than on the other sites in the second year, but declined to levels similar to the other sites in the third

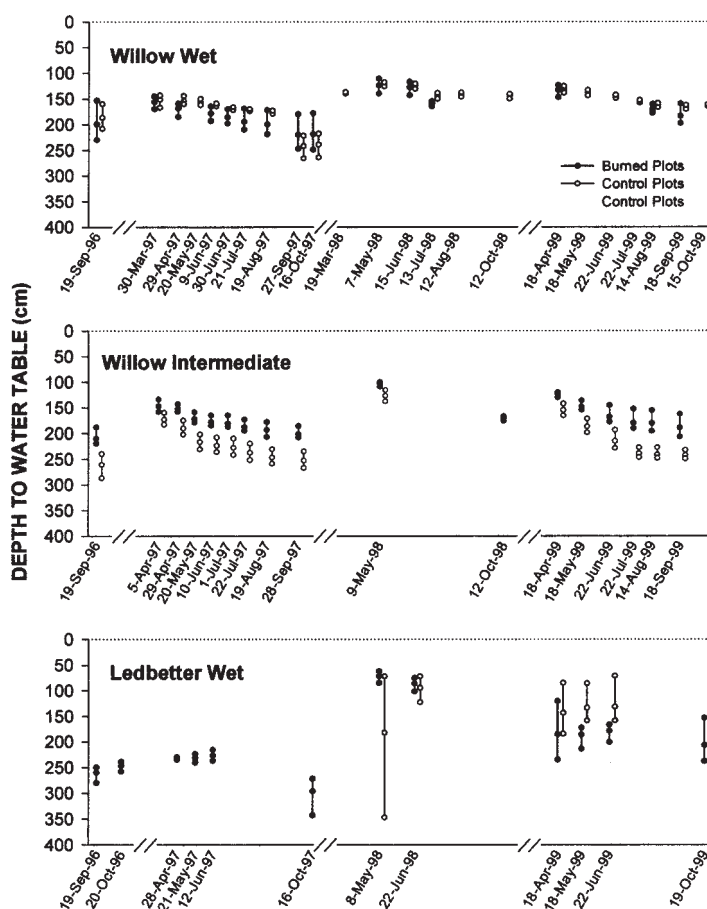


Fig. 1. Depth of the water table (max., mean, min.) for the three study sites from 19 September 1996 to 19 October 1999.

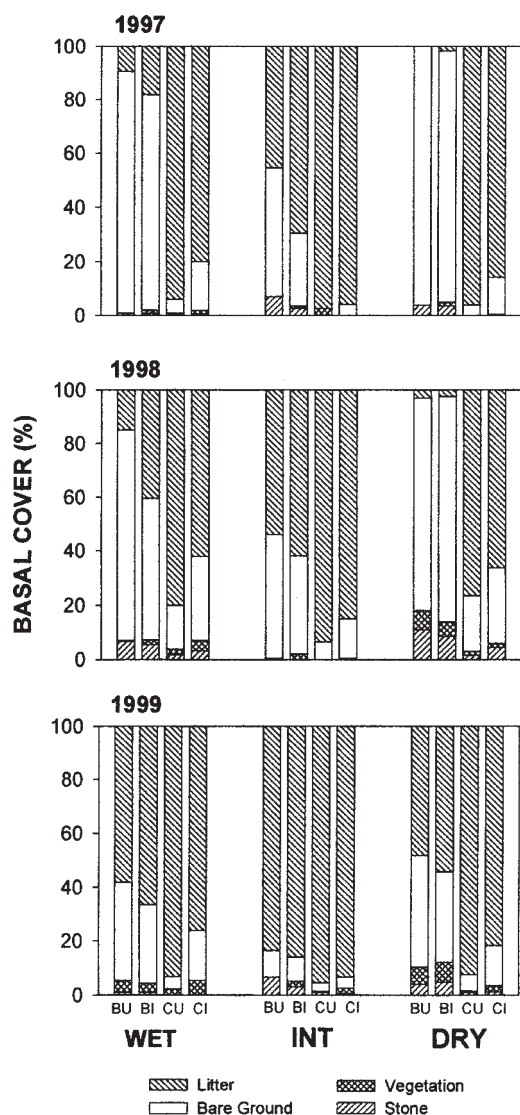


Fig. 2. Basal cover (bare ground, litter, stone and vegetation) in 1997, 1998 and 1999 for the wet, intermediate and dry sites. BU = burned under shrub; BI = burned interspace; CU = control under shrub; CI = control interspace.

year. On control plots, biomass of the wet sites did not differ from that of the intermediate site. Biomass of the dry sites was marginally lower than of wet or intermediate sites ($P < 0.1$).

In the first year, there were no differences in total biomass between burned and control plots. In years two and three biomass was more than twice as high on burned than control plots (year*treatment, $F_{2,16} = 9.05$, $P = 0.0023$). Burned interspace microsites had higher biomass than burned under shrub microsites for all water tables in 1997 and 1998 (water table*microsite, $F_{2,16} = 0.59$, $P = 0.5964$). By 1999, there were no significant differences between microsites. In general, control interspace microsites did not differ from control

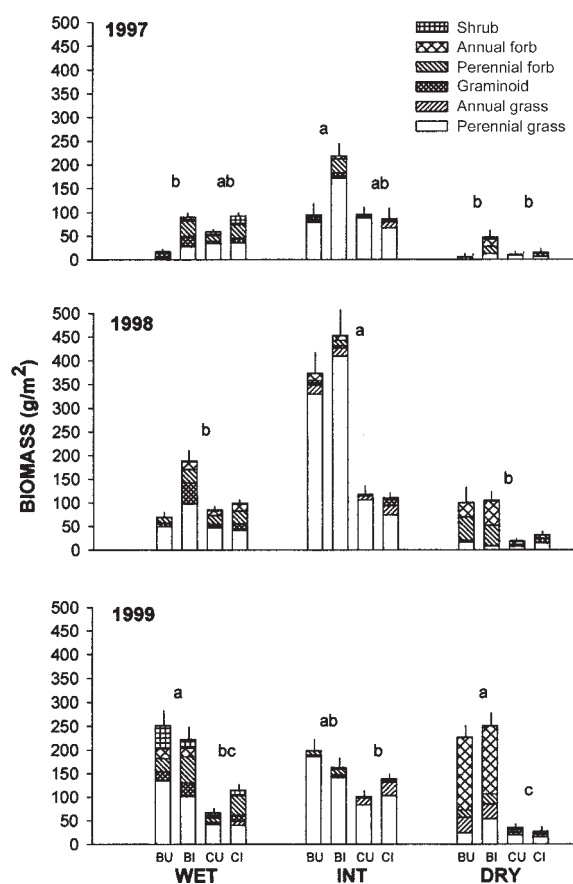


Fig. 3. Total biomass, delineated by life form, in 1997, 1998 and 1999 for the wet, intermediate and dry study sites. BU = burned under shrub; BI = burned interspace; CU = control under shrub; CI = control interspace. Values are means \pm s.e. Different letters indicate significant differences ($P \leq 0.05$) among microsites and water tables for 1997 and 1999, and between water tables for 1998.

under shrub microsites.

Pre-burn (1996) *Artemisia* volume was highest in the intermediate site followed by the dry sites and then the wet sites (water table, $F_{2,2} = 54.70$, $P = 0.0180$) (Fig. 4). There were no differences in pre-burn *Chrysothamnus* volume among water tables (water table, $F_{2,2} = 0.75$, $P = 0.5725$). Following the burn, there were no differences in volume among water tables or microsites for either *Artemisia* (water table*microsite, $F_{2,2} = 0.04$, $P = 0.9645$) or *Chrysothamnus* (water table*microsite, $F_{2,2} = 1.67$, $P = 0.3749$).

Life form and species responses

Perennial grass biomass increased progressively over the 3-yr study (year, $F_{2,16} = 17.60$, $P = 0.0001$). Perennial grasses comprised most of the total biomass in both wet and intermediate sites but were a minor component on dry sites (water table, $F_{2,2} = 70.32$, $P = 0.0140$) (Fig. 3). Burned interspace microsites had higher perennial grass biomass than burned under shrub microsites (treatment*microsite, $F_{1,4} = 34.28$, $P = 0.0042$). On control sites, perennial grass biomass was similar among years and did not differ among water tables or between microsites. Individual species responses to burning varied by water table and microsite (Table 2). In 1999, on wet and intermediate sites, *L. triticoides* a species typical of the dry meadow ecological type that spreads by rhizomes, had higher mean biomass on burned than control plots (Table 2). *Poa secunda* ssp. *juncifolia*, a bunchgrass found only on the wet sites, had higher biomass following burning especially on burned under shrub microsites (Table 2). *Leymus cinereus*, a seeded species typical of the *Artemisia/L. cinereus* ecological type that spreads by seed, had higher biomass on burned than control plots (Table 2). This species also had the highest biomass of any of the perennial grasses and sedges on the dry sites. *Carex douglasii*, a rhizomatous sedge species, had higher biomass following burning on wet sites but only in interspace microsites (Table 2).

In general, perennial forb biomass was higher in year three than in years one and two (year, $F_{2,16} = 4.24$, $P = 0.0333$) and was highest in interspace microsites of both burned and control plots (microsite, $F_{1,4} = 25.49$, $P = 0.0072$) (Fig. 3). *Lupinus argenteus*, a perennial forb with greatest abundance on wet sites, had higher biomass in interspace microsites both before and after the burn (Table 2). *Linum lewisii*, a seeded species, increased following the burn on wet and dry sites (Table 2).

Annual grass biomass was higher in years two and three than in year one on control plots of the intermediate site (year*water table*treatment, $F_{4,16} = 3.47$, $P = 0.0320$) (Fig. 3). Annual forb biomass was higher on dry sites in years two and three than year one, but only on burned plots (year*water table*treatment, $F_{4,16} = 6.49$, $P = 0.0027$) (Fig. 3). For example, on the Willow dry site 1999 biomass of *Descurainia pinnata* was only 3.3 g m⁻² on control plots, but was 104.7 g m⁻² on burned plots (Table 2). On the Marysville dry site, *Chenopodium album* biomass was 35.1 g m⁻² on burned plots and 0.0 g m⁻² on control plots (Table 2).

Shrub biomass was higher on wet than on dry or intermediate sites with burned interspace microsites having greater biomass in year one and burned under shrub microsites having greater biomass in year three (year*water table*treatment, $F_{4,16} = 3.74$, $P = 0.0247$)

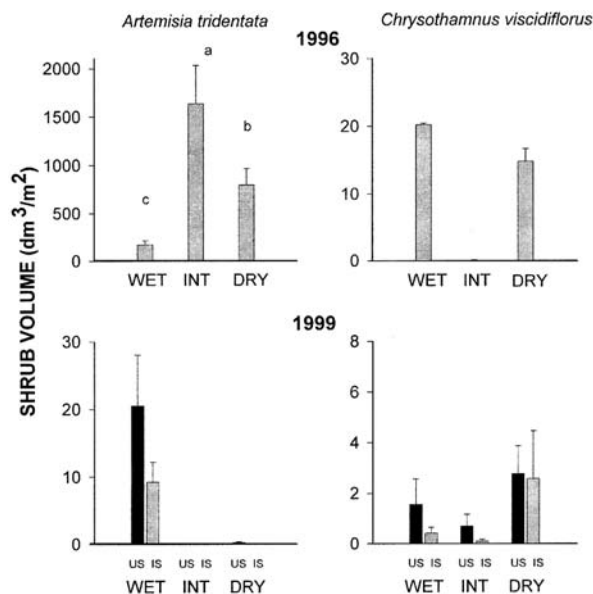


Fig. 4. Pre-burn (1996) and post-burn (1999) volumes for *A. tridentata* var. *tridentata* and *Chrysothamnus viscidiflorus*, for the wet, intermediate and dry sites. US = under shrub; IS = interspace; BU = burned under shrub; BI = burned interspace; CU = control under shrub; CI = control interspace. Values are mean + SE. Different letters indicate significant differences ($P < 0.05$) among water tables.

(Fig. 3). Seedling establishment of *Artemisia* was moderately high on burned wet sites, but total biomass was minimal. Total biomass for *Chrysothamnus viscidiflorus* (a root sprouting shrub) was higher on burned plots, especially in under shrub microsites (Table 2).

Spearman rank correlation analysis comparing third-year species composition of microsites within water tables showed that burning resulted in a re-apportionment of biomass among species (Table 3). While microsites within burned plots and microsites within control plots were highly similar, there were few similarities between burned and control microsites.

Table 3. Spearman's Rank Correlations (R_s) comparing third-year mean biomass of microsites within water tables (based on biomass of the 15 most abundant species) (BU = Burned Under shrub; BI = Burned Interspace; CU = Control Under shrub; CI = Control Interspace).

Water table	BU vs BI	BU vs CU	BU vs CI	BI vs CU	BI vs CI	CU vs CI
Wet	0.80***	0.28	0.02	0.26	0.22	0.73**
Intermediate	0.74**	0.48	0.49	0.63*	0.62*	0.99****
Dry	0.96****	0.14	0.12	0.22	0.05	0.83****

* = $P \leq 0.05$; ** = $P \leq 0.01$; *** = $P \leq 0.001$; **** = $P \leq 0.0001$

Table 2. Year three (1999) mean biomass (gm^{-2}) and the increase or decrease in biomass from 1997 to 1999 (in parentheses), by water table and microsite, for the 20 most abundant species sampled in the wet, intermediate, and dry sites. BU = burned under shrub; BI = burned interspace; CU = control interspace; CI = control interspace).

Life form	Wet sites				Intermediate site				Dry sites			
	BU	BI	CU	CI	BU	BI	CU	CI	BU	BI	CU	CI
Perennial grasses												
<i>Agropyron</i> spec.	2,6 (+ 1,6)	2,4 (+ 1,8)	4,8 (+ 4,6)	8,1 (+ 8,1)	0,9 (+ 0,9)	0,0	0,0	0,0	8,0 (- 2,6)	12,2 (+ 11,2)	1,4 (+ 1,1)	4,1 (+ 4,1)
<i>Elymus elymoides</i>	10,1 (+ 6,1)	11,3 (+ 7,5)	10,3 (+ 7,4)	4,3 (+ 3,2)	0,0 (- 0,3)	0,0	0,0	0,0	0,0 (- 1,9)	0,3 (- 0,1)	4,1 (+ 4,1)	2,4 (+ 2,4)
<i>Leymus cinereus</i>	49,6 (+ 37,4)	9,1 (+ 4,9)	3,5 (+ 3,5)	0,0	13,1 (- 6,2)	5,7 (+ 5,7)	0,0	0,0	6,3 (+ 6,3)	27,5 (+ 27,5)	0,0	1,2 (+ 1,2)
<i>Leymus triticoides</i>	51,5 (+ 36,0)	63,2 (+ 62,0)	0,0 (- 1,1)	0,0 (- 0,2)	150,6 (+ 38,1)	100,6 (+ 33,8)	46,1 (+ 2,2)	48,6 (+ 18,3)	9,2 (+ 4,7)	6,6 (+ 2,2)	12,1 (+ 11,3)	6,4 (+ 6,4)
<i>Muhlenbergia richardsonis</i>	0,7 (- 1,3)	0,3 (+ 0,3)	0,0	5,8 (+ 5,8)	0,0	0,0	0,0	0,0	0,5 (- 0,5)	7,2 (+ 7,2)	0,0	0,0
<i>Poa pratensis</i>	0,0 (- 1,0)	1,1 (+ 0,8)	0,0	0,0	21,5 (- 31,8)	35,2 (- 1,3)	33,3 (+ 14,5)	50,5 (+ 37,1)	0,0	0,0	0,9 (+ 0,9)	0,6 (+ 0,6)
<i>Poa secunda</i> ssp. <i>juncifolia</i>	17,3 (+ 8,6)	2,1 (- 2,6)	10,0 (+ 7,5)	7,0 (+ 6,1)	0,0 (- 5,8)	0,0 (- 2,8)	0,0 (- 0,2)	0,0	0,0	0,0	0,0	0,0
<i>Poa secunda</i> ssp. <i>secunda</i>	3,1 (- 10,6)	11,5 (+ 3,4)	13,1 (+ 9,2)	12,7 (+ 11,9)	0,0 (- 3,7)	0,0 (- 2,8)	3,7 (+ 2,8)	3,6 (+ 3,6)	0,0 (- 1,9)	0,0 (- 0,6)	1,2 (+ 1,2)	0,6 (+ 0,6)
Annual grasses												
<i>Bromus tectorum</i>	0,6 (+ 0,6)	0,3 (+ 0,3)	0,4 (+ 0,4)	9,0 (+ 9,0)	3,0 (- 10,7)	3,5 (- 1,3)	15,0 (+ 11,5)	28,4 (+ 27,2)	32,5 (+ 32,5)	30,3 (+ 30,3)	0,0	0,3 (+ 0,3)
Sedges and rushes												
<i>Carex douglasii</i>	13,7 (- 7,2)	22,4 (+ 13,3)	2,6 (- 1,5)	9,8 (+ 6,7)	0,0 (- 5,5)	1,4 (- 1,1)	2,4 (+ 0,2)	2,7 (+ 1,4)	0,0 (- 7,3)	1,0 (+ 0,4)	6,0 (+ 6,0)	9,3 (+ 9,3)
<i>Juncus balticus</i>	4,2 (+ 3,2)	5,2 (+ 4,3)	1,5 (+ 0,6)	2,0 (+ 1,4)	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0
Perennial forbs												
<i>Erigeron pumilus</i>	2,5 (+ 0,2)	3,9 (+ 2,7)	1,8 (+ 0,9)	10,0 (+ 10,0)	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0
<i>Iva axillaris</i>	1,6 (- 4,9)	1,2 (+ 0,9)	0,0	3,8 (+ 3,8)	8,3 (- 15,1)	7,3 (+ 2,6)	0,2 (+ 0,2)	0,8 (+ 0,8)	0,0 (- 0,4)	0,0 (- 0,3)	0,0	0,0
<i>Linum lewisii</i>	1,4 (+ 1,4)	3,8 (+ 3,8)	0,0	0,0	0,0	0,0	0,0	0,0	9,4 (- 4,5)	13,6 (+ 8,9)	0,0	0,0
<i>Lupinus argenteus</i>	15,9 (- 10,5)	41,7 (+ 23,4)	4,9 (- 1,8)	21,4 (+ 15,2)	0,0 (- 3,1)	0,0	0,0	0,0	0,0 (- 0,2)	0,0	4,5 (+ 4,5)	4,4 (+ 4,4)
<i>Marrubium vulgare</i>	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	6,1 (+ 6,1)	7,2 (+ 7,2)	0,0	0,0
Annual forbs												
<i>Chenopodium album</i>	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	27,0 (+ 27,0)	43,2 (+ 43,2)	0,0	0,0
<i>Descurainia pinnata</i>	14,8 (+ 14,5)	12,1 (+ 12,1)	0,0	0,0	0,4 (- 0,2)	0,6 (+ 0,1)	0,0	3,3 (+ 3,3)	117,4 (+ 117,1)	92,0 (+ 92,0)	3,3 (+ 3,3)	3,2 (+ 3,2)
Shrubs												
<i>Artemisia tridentata</i> ssp. <i>tridentata</i>	5,1 (+ 3,3)	0,9 (+ 0,6)	0,9 (+ 0,9)	1,0 (+ 1,0)	0,0	0,0	0,0	0,0	1,4 (+ 1,4)	1,0 (+ 1,0)	0,0	0,0
<i>Chrysothamnus visidiflorus</i>	44,2 (+ 29,8)	18,0 (+ 13,1)	8,6 (+ 4,3)	9,6 (+ 7,1)	0,0 (- 2,6)	0,0	0,0	0,0	0,0 (- 4,1)	0,0 (- 1,1)	0,2 (+ 0,2)	2,9 (+ 2,9)

Discussion

The responses of the different sites to the restoration treatments combined with our knowledge of these ecosystems can be used to identify the alternative states and define the thresholds that exist for *Artemisia* dominated riparian corridors in the central Great Basin (Fig. 5). The water table regimes and abundance of shrubs indicated that the study sites were at the lower end of the water table depths necessary to support the dry meadow ecological type. As described by Weixelman et al. (1996), the dry meadow type is characterized by grasses and sedges and has depths to soil saturation of 70 to 100 cm in June and July. Water table depths necessary to produce soil saturation at 70 to 100 cm were reached only in spring and early summer of 1998 on the wet and intermediate sites (Fig. 1). As originally described, the relatively high water tables of the dry meadow type facilitate the establishment and persistence of species such as *P. secunda* ssp. *juncifolia* that are adapted to mesic conditions. Saturated rooting zones during the spring and early summer prevent the establishment and persistence of *A. tridentata* ssp. *tridentata* and other shrubs (see Ganskopp 1986). Overgrazing and other perturbations can alter species composition of the dry meadow ecological type (Weixelman et al. 1997), but will not change the physiognomy unless the water table drops.

The wet and intermediate study sites appear to represent an alternative state of the dry meadow ecological type (Fig. 5). Three years after the burn the biomass and species composition of the wet and intermediate sites were largely within the parameters that characterize the dry meadow type (Weixelman et al. 1996). Plant community composition was determined primarily by understorey species that survived the burn and that were capable of regrowth, such as *P. secunda* ssp. *juncifolia* and the rhizomatous grass *L. triticoides*. The wet and intermediate sites are characterized by relatively low water tables (– 50 to – 250 cm) and are susceptible to *Artemisia* encroachment. Occasional high water tables coupled with favourable environmental conditions can facilitate episodic establishment of species typical of the dry meadow type as occurred on our sites in 1998, a high precipitation year (Chambers & Linnerooth 2001). However, water tables are sufficiently low that *Artemisia* seedlings can establish and persist, as was observed on the wet sites. Overgrazing of this alternative state presumably increases *Artemisia* establishment by reducing competition from the herbaceous species (see Belsky et al. 1999). Once *Artemisia* has established, fire is necessary to remove the shrub and return the state to graminoid and forb dominance.

Sites with the lowest water tables (– 250 to >– 300 cm) are dominated by *Artemisia* with a minor component of

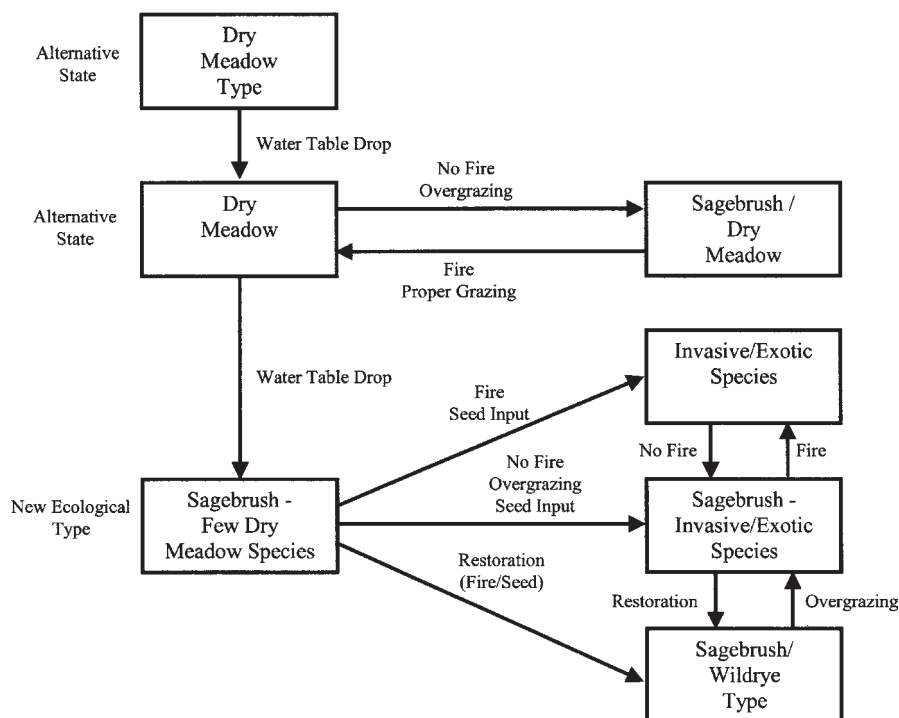


Fig. 5. Diagram of the states and transitions existing in riparian dry meadow ecosystems in central Nevada. Sagebrush = *Artemisia tridentata* ssp. *tridentata*; Wildrye = *Leymus cinereus*.

the species that typify the dry meadow ecological type (Fig. 5). These sites have crossed an abiotic threshold and no longer have the potential to support the dry meadow site type. Although total biomass on dry sites was similar to that on wet sites, the above-ground vegetation was dominated by the annual forbs that characterized the seed banks of both wet and dry sites (Wehking 2002). For example, in 1997 and 1998 *Nicotiana attenuata*, a fire-dependent annual (Baldwin & Morse 1994), dominated the Willow dry burned site, but in 1999 another annual forb, *Descurainia pinnata*, dominated. These sites are currently unstable and can exhibit several different pathways depending on the disturbance regime and initial species composition. As occurred on our sites, fire can convert these states to invasive/exotic grasses and forbs, such as *Bromus tectorum* or *D. pinnata* (Table 2). In the absence of fire, overgrazing and the introduction of invasive/exotic species can result in co-dominance by *Artemisia* and these species (pers. obs.). Establishment of *Artemisia* and seeded *L. cinereus* on the dry sites (Table 2) indicates that these sites have the potential to support at least the more xeric species that characterize the *Artemisia/L. cinereus* ecological site type (Weixelman et al. 1996). Active restoration would be required as the herbaceous understorey species that characterize the *Artemisia/L. cinereus* ecosystem type are almost non-existent on the dry sites (Table 2).

Burning resulted in the competitive release of the understorey species and was an effective restoration treatment on the wet and intermediate sites. Following burning both wet and dry sites had increased soil water content at depths ≥ 30 cm (Chambers & Linnerooth 2001) and higher levels of plant available nutrients including sulphate, potassium and ammonium (Blank et al. in press). Herbaceous biomass increased over time on burned plots, while understorey biomass on control plots remained the same. Although vegetative response on burned interspace microsites was initially greater than on burned under shrub microsites, these differences became non-significant over time. Initial microsite differences can be attributed to higher soil temperatures (as indicated by ash colour) in under shrub than interspace microsites (Blank et al. 1998) and higher mortality of both plant meristems and seeds (Wehking 2002).

Knowledge of the alternative states and thresholds that exist for these riparian corridors can be used to design restoration schemes aimed at creating a mosaic of *Artemisia* and dry meadow ecosystems that more closely resembles predisturbance conditions. Areas that are currently dominated by *Artemisia* but have the potential to support the grass and sedge dominated alternative stable state can be identified on the basis of

water table depths and understorey species composition. Restoration that includes prescribed burning and proper management can be used to restore these areas to sedge and grass dominance with minimal intervention and expense. Sites that have the potential to support the *Artemisia/L. cinereus* ecological type can also be identified. Active restoration techniques including burning, eliminating the invasive/exotic species if present and seeding with the appropriate species complement can be used to establish this ecological type. The investment required to establish this type is significantly greater than that required for restoring the grass and sedge dominated alternative state of the dry meadow. The decision to both restore the graminoid dominated state of the dry meadow ecological type and establish the *Artemisia/L. cinereus* type will require both economic and ecological analyses.

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